

ON THE SOURCE OF THERAPSIDS

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(With 2 plates, 5 figures and 1 table)

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INTRODUCTION

The very fragmentary evidence of therapsids in North America during the Permian has provided interesting but uncertain information concerning the geographic distribution of this order and the times of origin of different evolutionary lines. Many questions were raised in a general report (Olson 1962), but few of them have been touched on more than lightly since that time. They were summarized as far as possible in my recent book (Olson 1971: 641-655). Some aspects of the problems have been treated by Chudinov, in particular in Sigogneau & Chudinov (1972).

Discovery of vertebrates in the Chickasha Formation, Guadalupian of Oklahoma (Olson 1965), has added information. A better understanding of the vertebrates of the Cutler and Abo Formations, Wolfcampian of northern New Mexico and south-western Colorado, through the work of Vaughn (1966, 1969a, b) and Lewis & Vaughn (1965) has given new insights into the significance of this faunal complex. Together these studies have produced substantial evidence of faunal assemblages which evolved largely independently of those of south-western New Mexico, Texas, and Oklahoma. The latter have been grouped into what has been termed the Permo-Carboniferous Chronofauna; the former assemblages have been termed the Caseid Chronofauna (Olson 1971: 839, fig. 145E). Only recently has it been determined that the Caseid Chronofauna has any relationship to the origin of therapsids.

Study of a new specimen found during the summer of 1972 in the Chickasha Formation revealed that it is not, as informally reported at the time of discovery, a somewhat therapsid-like sphenacodontine, but rather that it is a very primitive gorgonopsian. The implications of this find are, of course, manifold and form an important part of the substance of this paper. Following a descrip-

tion of the new animal, they are considered in relationship to the broader problem of the source of therapsids.

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A NORTH AMERICAN GORGONOPSIAN

Class **REPTILIA**
 Subclass **SYNAPSIDA**
 Order **THERAPSIDA**
 Suborder **GORGONOPSIA**
 Family **Gorgonopsidae**
Watongia gen. nov.

Diagnosis: A very primitive, sphenacodont-like gorgonopsian reptile. Estimated body length 1,22 to 1,52 metres. Skull with large preparietal bone. Ten to 12 simple, recurved, conical cheekteeth, diminishing in crown height from anterior to posterior; a large, anterior, canine-like tooth.

Vertebrae with centra relatively short (see measurements, Table 1), deeply amphicoelous and sharply keeled. Neural arch with a deep pit on either side above the diapophysis. Neural spine slender, height about equal to $\frac{1}{2}$

TABLE 1

Measurements of *Watongia meieri* gen. et sp. nov. in millimetres.

| VERTEBRAE | 1 | 2 | 3 | 4 |
|---------------------------------------|--------|----|----|------|
| Length, centrum, basal | 21 | 20 | — | — |
| Total height, anterior | 85 | — | — | — |
| Height neural spine, anterior | 43 | — | — | — |
| Width posterior zygapophyses | 26 | 27 | — | — |
| Length diapophysis, dorsal | — | 12 | 12 | 14 |
| LIMB BONES | L | PW | DW | WS |
| Humerus | 125 | 65 | — | 16* |
| Radius | 89 | 18 | 19 | 10** |
| Ulna | 116*** | 33 | 30 | 17 |

Abbreviations: L, maximum length; PW, maximum proximal width;

DW, maximum distal width; WS, minimum shaft width. *—with ventral surface dorsal; **—anterior view;

***—including olecranon process.

of total vertebral height. Diapophysis short, stocky and with heart-shaped articular surface. Posterior cervical and anterior dorsal ribs with tuberculum somewhat reduced and not fully separated from capitulum.

Scapula moderately high and narrow; cleithrum present but very slender. Humerus lightly structured with well-defined shaft and angle between two 'blades' of about 60 degrees. Carpus with very large, pisiform element; distal

5 present and not fused with distal 4. Phalangeal formula 2?453, with distal phalanges rather short and unguals strongly claw-shaped.

The name is after the town of Watonga, Blaine County, Oklahoma.

Watongia meieri sp. nov.

Holotype: UCLA VP 3132. Part of the frontal-parietal region of the skull, including the dorsal part of the orbital margin and fragments of the maxilla with teeth in place. Three anterior dorsal vertebra with fragments of others. Left scapula and part of right; left clavicle; part of left cleithrum; and part of interclavicle. Several ribs and numerous gastralia. Right and left fore limbs with carpus and partial complement of phalanges.

Horizon and locality: Chickasha Formation, level of middle part of Flowerpot Formation, El Reno Group, Guadalupian, Upper Permian. From fossil site BC 7 (Olson 1965), NW. $\frac{1}{4}$, NE. $\frac{1}{4}$, Sec. 33, T. 18 N., R. 11 E., Blaine County, Oklahoma. The species name is given for Mr Meier of Hitchcock, Oklahoma, on whose land the specimen was found.

Description: The specimen was found somewhat scattered in red, sandy shale. It lay near the base of a gently dipping deposit formed in a stream channel. Only the anterior part was found; the skull had weathered out and much of it had disintegrated and disappeared. At about the same level in this site have been found specimens of *Rothianiscus* and *Cotylorhynchus*.

1. *Skull*: Figure 1B, Plate IA, B. Part of the skull roof and fragments of the maxilla are all that have been preserved. The most significant feature is the presence of a large preparietal bone in the skull roof. There were about 12 teeth in the postcanine series. The exact number is uncertain for some of the fragments cannot be certainly placed in the series. The teeth appear to have decreased regularly in crown height from anterior to posterior. A single 'canine' is present. Its height is estimated as 20 to 25 mm, somewhat more than twice the height of the longest postcanine. Skull length is estimated to have been about 24 to 26 cm on the assumption that proportions were more or less those of *Dimetrodon*.

2. *Vertebrae*: Figure 2A, B, Plate IID. Three anterior dorsal vertebrae and fragments of others have been recovered. Many of the features are those found in sphenacodonts. Neural spines, however, are not elongated or heavy as in sphenacodontines. Centra are strongly keeled, deeply amphicoelous and not elongated. Measurements in Table 1 show the major dimensions. Transverse processes are relatively short and thick and terminate in stout, heart-shaped articular surfaces. Above the diapophysis on each side, as in sphenacodontines, the neural arch has a deep pit on its lateral surfaces. A small intercentrum is present on the anterior margin of one of the vertebrae.

3. *Ribs*: Figures 1 EF, 2D; Plate IIE. The ribs are slender and gently curved. Comparisons of the shapes of the heads with those of sphenacodonts and gorgonopsians are shown in Figure 2D. The structure of the head is some-

what more like that in gorgonopsians, with the tuberculum reduced and the bifid character much less well expressed than in sphenacodonts. Tooth-pick shaped gastralria were found scattered throughout the deposit in the vicinity of the specimen, Plate IIA, B.

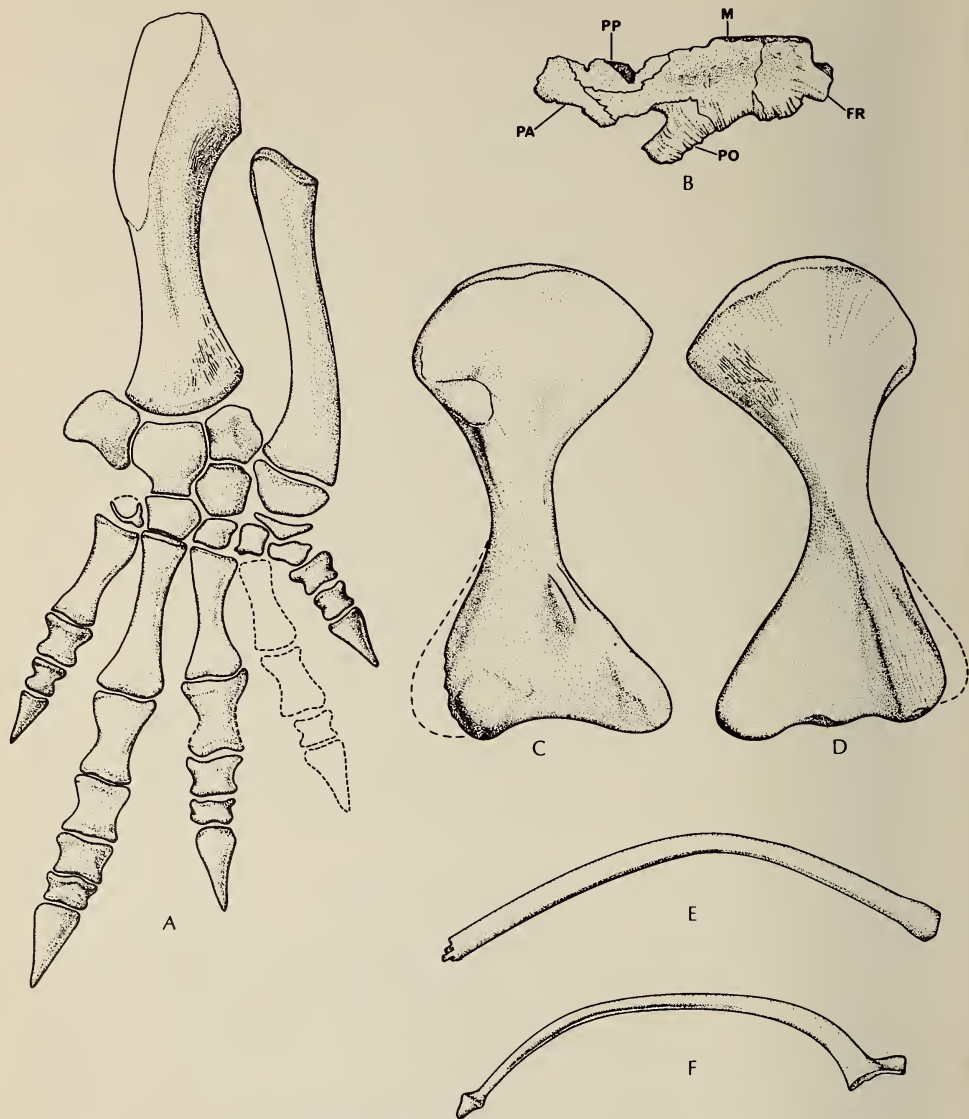


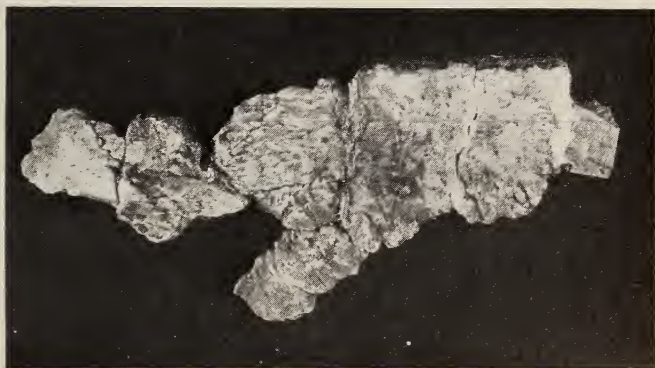
Fig. 1. *Watongia meieri* gen. et sp. nov.

A. Reconstruction of the left lower limb, based on data from both right and left. B. Skull fragment, showing midline, orbital margin and preparietal element. C. Right humerus, dorsal. D. Right humerus, ventral. E. Dorsal rib, head missing. F. Anterior dorsal rib. Abbreviations: FR, frontal; M, midline; PA, parietal; PO, post-orbital; PP preparietal. All $\times \frac{1}{2}$.

4. *Shoulder girdle*: Figure 3A, B. A somewhat broken left scapula, part of the right scapula, a partial left clavicle, a cleithrum and part of the interclavicle provide the information on this part of the skeleton. The scapula is



A



B

PLATE I. *Watongia meieri* gen. et sp. nov.

A. Fragments of jaws and teeth in medial aspect. Lower set roughly in order in jaw. B. A fragment of the dorsal platform of the skull showing the preparietal bone. See Fig 1B for identification of elements. Midline of skull to top of page and anterior to the right. Both $\times 1$.

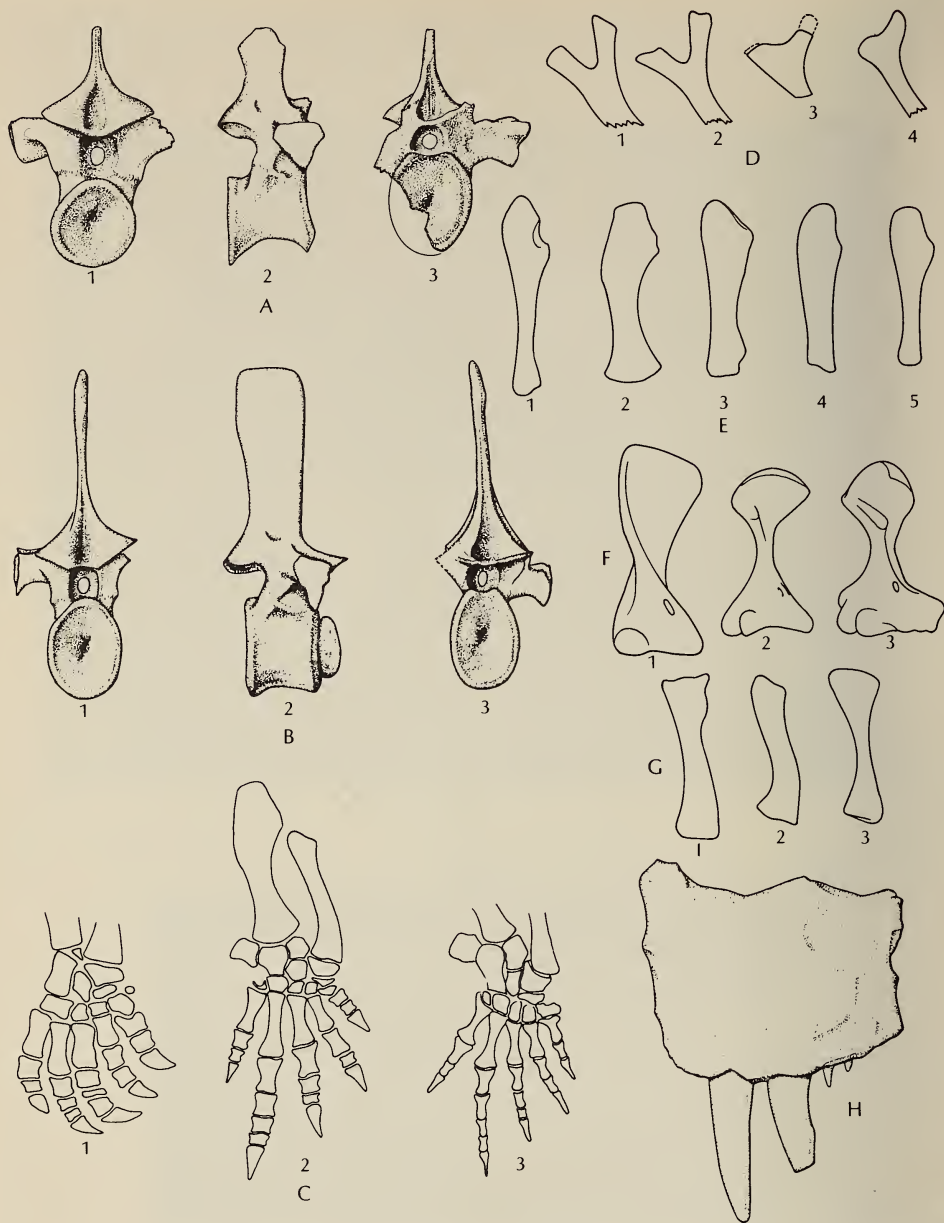


Fig. 2.

A. Anterior dorsal vertebra of *Watongia meieri* gen. et sp. nov.: 1. posterior, 2. lateral, 3. anterior. B. Anterior dorsal vertebra of *Watongia meieri* gen. et sp. nov.: 1. posterior, 2. lateral, 3. anterior. C. Manus: 1. *Aelurognathus* (Boonstra 1934), 2. *Watongia*, 3. *Dimetrodon* (Romer 1956). D. Heads of anterior dorsal ribs: 1. *Ctenospondylus*, 2. *Dimetrodon*, 3. *Watongia*, 4. gorgonopsian. E. Ulna: 1. *Dimetrodon* (Romer 1956), 2. *Watongia*, 3. *Gorgonops* (Broili & Schroeder 1935), 4. *Aelurognathus* (Boonstra 1934), 5. *Lycaenops* (Colbert 1948). F. Humerus: 1. gorgonopsian, 2. *Watongia*, 3. *Dimetrodon* (Romer 1956). G. Radius: 1. *Dimetrodon* (Romer 1956), 2. *Watongia*, 3. *Aelurognathus* (Boonstra 1934). H. *Knoxosaurus* (Olson 1962). A and B $\times \frac{1}{2}$.



PLATE II. *Watongia meieri* gen. et sp. nov.

A. Right lower limb and carpus. Reconstructed part of ulna in white based on impression in the enclosing matrix. B. Left fore limb including carpus and manus. Under side of limb with digits flexed. Radius absent. C. Right humerus in ventral aspect. D. Anterior dorsal vertebra, from left side. E. Anterior cervical rib. All $\times \frac{3}{8}$.

high, rather narrow, and the cleithrum is small. The most distinctive feature of the scapula is a strong rugosity on the inner surface adjacent to the area of attachment of dorsal part of the clavicle. This extends inward over about $\frac{1}{3}$ of

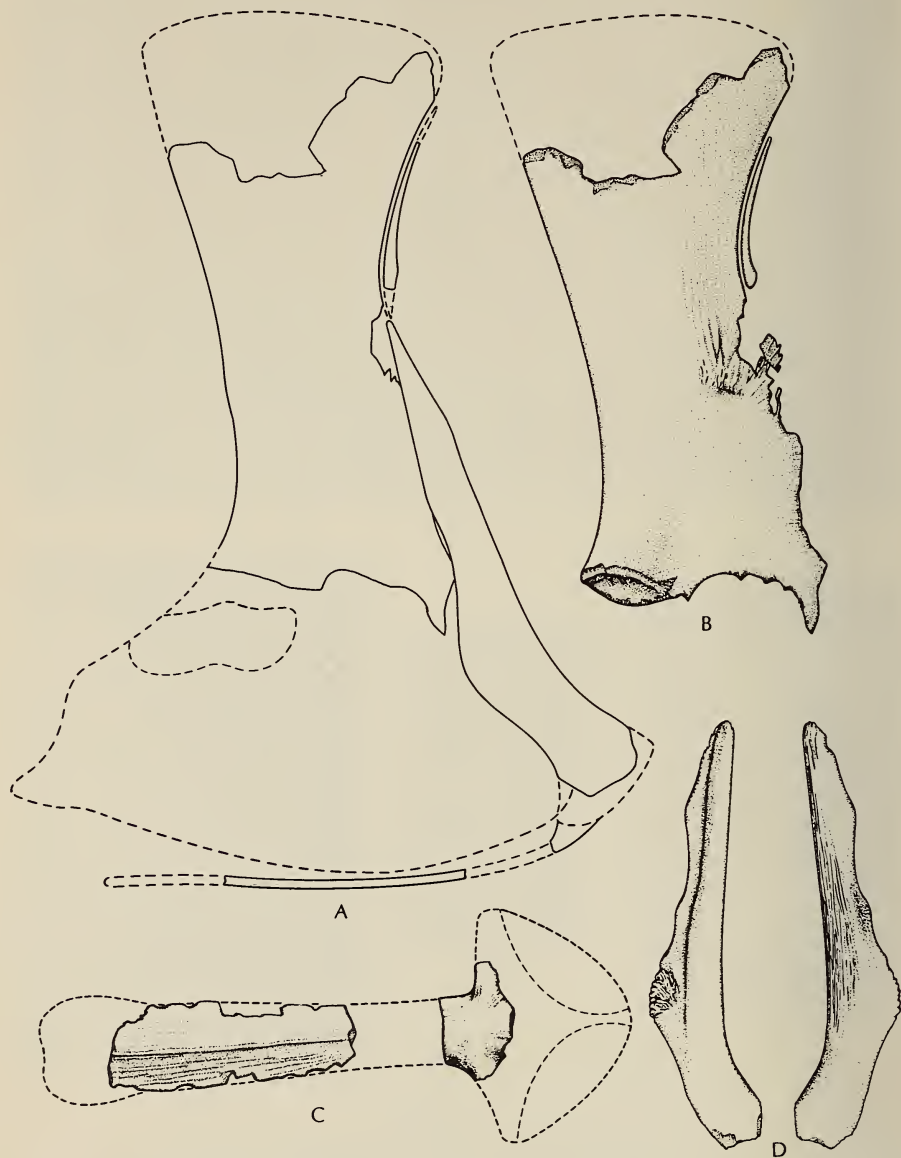


Fig. 3. *Watongia meieri* gen. et sp. nov.

A. Reconstruction of right shoulder girdle. B. Left scapula and part of cleithrum, inner side. C. Interclavicle, preserved parts and suggested relationships in reconstruction. D. Clavicle, left inner and outer aspects. All $\times \frac{1}{2}$.

the scapular blade and carries dorsally in a slightly depressed area marked by vertical striae. Apparently this represents an area of insertion of ligaments from the clavicle, although the area seems excessively extensive for such ligaments. It is possible that it marks the insertion of tendons of a large, levator scapulae which invaded the inner surface of the scapula. Again, the extent is considerably greater than would be expected. Various pelycosaurs and primitive therapsids have a somewhat similar small area of striated markings in this vicinity, but the development is much less. The functional significance in the new animal remains uncertain.

The clavicle and interclavicle, as shown in Figure 3C, D, fall well within the range of structures found among the pelycosaurs and primitive therapsids and have few unusual features. At the level of flexure between the shaft and ventral blade of the clavicle the anterior and inner margin of the bone has a strongly rugose surface, much like that on the inner surface of the scapula. Presumably this also was the site of attachment of ligaments.

5. *Fore limbs*: Figures 1A, 2C, E, F, G; Plate IIA, B, C. Most features are well shown in the figures and plates. Comparisons with sphenacodonts and gorgonopsians are shown in outline in Figure 2C and measurements are given in Table 1. It will be seen from these that in general the limb elements are intermediate between sphenacodonts and gorgonopsians, with the humerus, radius and ulna somewhat more like comparable bones in the latter and the manus closer to that of sphenacodonts.

The humerus is lightly built. The right humerus is well preserved and the left is crushed. The two blades in the right make an angle of about 60 degrees with each other. The deltopectoral crest has a well-developed boss for the insertion of the pectoralis muscle but is rather weak distally. The ectepicondyle is strong but the supinator process, which is not well preserved in either humerus, appears to have been weak. The entepicondyle is strong but is not greatly expanded. An entepicondylar foramen is present, but is not visible in dorsal aspect. No ectepicondylar foramen has been identified. The area in which it would be, were it present, is damaged and its existence is not out of the question.

The radius is slender, curved and slightly twisted along the long axis. It is much more like the radii of primitive therapsids than those found in sphenacodonts. The ulna is thick relative to its length. The olecranon process is moderately developed and the distal end of the ulna is broad. Except for the last feature, the ulna resembles that of various gorgonopsians, Figure 2E. It is not basically sphenacodont in its principal features.

The carpus, metacarpus and phalanges are preserved, mostly intact as shown in Plate IIA, B. The carpus is basically sphenacodontine in character. Distals 4 and 5 are not fused. Fusion is indicated in all figures of the gorgonopsian carpus. Were it not for the presence of a remnant of distal 5 in *Watongia*, this interpretation would undoubtedly have been made, for the shape of distal 4 is essentially that of the supposedly fused element in various primitive therapsids.

The pisiform is extremely large and presumably the tendon of the flexor musculature was unusually strong. This is in marked contrast to the known feet of gorgonopsians and the element is as strong as or stronger than in *Dimetrodon*.

The phalangeal formula apparently was of the primitive 23453 pattern, although the second digit has not been identified. There is only moderate reduction of the more distal phalanges, much as in *Dimetrodon* and the gorgonopsian, *Aelurognathus*, Figure 2C.

6. *Systematic position*: *Watongia* is placed with the Gorgonopsia primarily upon the undeniable presence of the preparietal. This element is present only among gorgonopsians and anomodonts and its form in the latter is quite different from that in the gorgonopsians. It is, of course, possible that it was developed independently in *Watongia* and gorgonopsians but, in view of the many other structures in which *Watongia* tends towards the gorgonopsian condition, it seems unlikely that this is the case.

The specimen shows a mosaic of sphenacodont and gorgonopsian characters. In it we find one of the rare instances of an almost ideal intermediate between two major groups, but one in which a definitive feature makes placement in one or the other plausible. Although solving an otherwise annoying taxonomic dilemma, the presence of the preparietal does not detract from the essentially intermediate nature of the *Watongia*.

The family Gorgonopsidae, as revised by Sigogneau (1970) has 22 genera which, while coherent in fundamental characteristics, have considerable variation in skull form, dentitions, and development of limb structure. The Russian gorgonopsians, *Amalitzkia* and *Inostrancevia* (Pravoslavlev 1927a, b), not treated by Sigogneau, fall within the gorgonopsids. Sigogneau recognized two subfamilies, Gorgonopsinae and Rubidgeinae. Major differences separate the two and it is to the former that *Watongia* bears close resemblance.

Much of the work on gorgonopsian systematics has treated skull structure and dentitions. The postcranium has not been studied for most genera so that the range of variation is not well known. Most of what is available is the result of work by Broom (1930), Broili & Schroeder (1935a, b), Boonstra (1924, 1953, 1963, 1965), Pravoslavlev (1927a, b), Colbert (1948) and the summary by Sigogneau (1970). Little is known of the postcranium of the oldest specimens from South Africa. Most generalized of the better known materials from later times appears to be *Aelurognathus* from the *Endothiodon* and *Cistecephalus* Zones. *Gorgonops* (Broili & Schroeder 1935a, b), from the base of the *Endothiodon* Zone is at much the same level, and *Lycaenops* (Colbert 1948) is much more advanced.

Watongia, although more primitive than any genus heretofore assigned, can be included in the family Gorgonopsidae and the subfamily Gorgonopsinae without seriously modifying the morphological limits given by Sigogneau.

CHRONOFAUNAS IN THE MID-CONTINENTAL UNITED STATES

The persistence and coherence of ecological systems during the late Pennsylvanian and early Permian of the United States is being increasingly documented. The vertebrate portions of these temporally persistent ecological systems have been termed chronofaunas, or more precisely vertebrate chronofaunas (Olson 1952, 1958). A useful way to view and study the evolution of particular phyla is in the chronofaunal context, and that is the approach used in the remainder of this paper.

The excellent record of lowland, deltaic vertebrates in North America is the basis for what has been termed the Permo-Carboniferous Chronofauna (Olson 1971: 645-654). This is characterized by an aquatic base of the food chain, with the large carnivore *Dimetrodon* standing at the peak of the pyramid. It is best known from Texas, Oklahoma and southern New Mexico, Figure 4. It ranges through the Wolfcampian and Leonardian, Figure 5. In the eastern

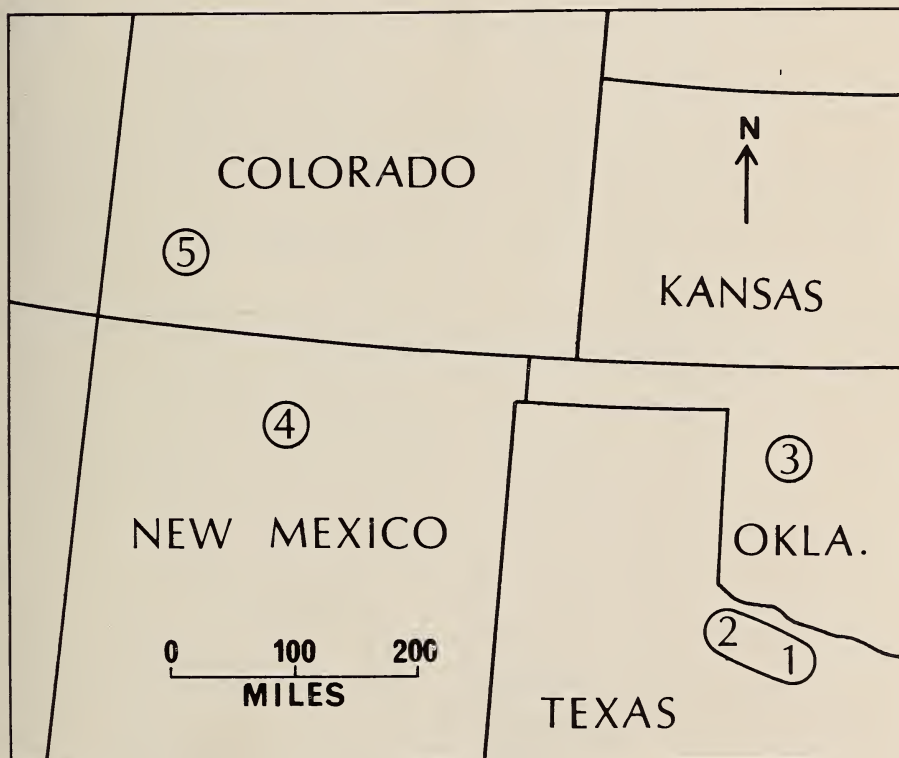


Fig. 4. Sketch map showing areas that have yielded specimens of Caseid Chronofauna as cited in text.

1. Lower Permian (Leonardian) of Texas. 2. Area of San Angelo Formation of Texas from which fossils have come. 3. Area of fossiliferous Chickasha beds of Oklahoma. 4. Northern New Mexico site. 5. The south-western Colorado site.

part of the United States, in Ohio, Pennsylvania, and West Virginia, a somewhat similar chronofauna exists. It is less well known and was partially isolated from the Permo-Carboniferous Chronofauna. European Autunian deposits, although showing little temporal continuity, indicate the existence of a generally similar system in the Old World during the very early Permian and, from what little is known, the early Permian vertebrates in many parts of the world were quite similar.

Less well known, but slowly becoming clearer, is a second chronofauna of the Mid-Continent area of the United States. This is the complex called

S. W. COLORADO
N. NEW MEXICO

TEXAS

OKLAHOMA

U. S. S. R.

| | | | | | | | |
|----------------------|-------------|-----------------|------------------|-----------------------------|-----------|---------------|----------|
| | GUADALUPIAN | PEASE RIVER GR. | DOG CREEK FM. | DOG CREEK FM. | KAZANIAN | ISHEEVO ZII | |
| | | | BLAINE FM. | BLAINE FM. | | CHICKASHA FM. | OCHER ZI |
| | | | FLOWER POT FM. | FLOWER POT FM. | | | |
| | LEONARDIAN | CLEAR FORK GR. | CHOZA FM. | HENNESSEY FM. | KUNGURIAN | | |
| | | | VALE FM. | GARBER FM. | | | |
| CUTLER - ABO FMS. | WOLFCAMPIAN | WICHITA GROUP | LEUDERS FM. | WELLINGTON FM. (WICHITA) | | | |
| | | | CLYDE FM. | | | | |
| | | | BELLE PLAINS FM. | | | | |
| | | | ADMIRAL FM. | | | | |
| | | | PUTNAM FM. | | | | |
| | | | MORAN FM. | | | | |
| | | | PUEBLO FM. | | | | |

Fig. 5.

A stratigraphic chart of the pertinent geological subdivisions and their temporal relationships.

the Caseid Chronofauna (Olson 1971). It existed in somewhat more upland circumstances (see Olson & Vaughn 1970) and is characterized by varanopsids, caseids, or caseid-like, primitive edaphosaurians, and the absence of *Dimetrodon*. Its basic characteristics relate to a food chain in which terrestrial reptiles, caseids and captorhinids, occupy the role of secondary producers. Predators include varanopsids, and haptodontine-sphenacodontine pelycosaurs, but not *Dimetrodon*.

Its earliest manifestation in the Permian record is in the Cutler and Abo Formations of northern New Mexico and south-western Colorado, Figure 4. Both the known faunas and the sedimentation support the conclusion that this is not a truly deltaic fauna, but one that lived somewhat more in uplands, and in the case of the Colorado fauna, near to highlands (Vaughn 1969b). This earliest phase has not produced caseids, although possible relatives, such as *Oedaleops* (Langston 1965) are known. *Sphenacodon* is present, *Aerosaurus*, very close to *Varanops*, is present in New Mexico, and in Colorado a haptodontine, *Cutleria*, has been found (Lewis & Vaughn 1965).

The youngest representation of this chronofauna is in the Chickasha Formation of Blaine County, Oklahoma. It is from this assemblage that the new gorgonopsian, *Watongia*, has come. In the same beds occur the caseids, *Cotylorhynchus* and *Angelosaurus*, the varanopsid, *Varanodon*, a captorhinid, *Rothianiscus*, and *Fayella*, a highly terrestrial dissorophid amphibian (Olson 1965, 1972). Both the Cutler-Abo and the Chickasha assemblages include other genera. The number of truly aquatic forms is low in both instances, although some are present.

It has long been apparent that the therapsids arose from among the pelycosaurs and largely if not entirely from the Sphenacodontidae. It is also evident that they did not arise from the principal sphenacodontid of the Permo-Carboniferous Chronofauna, *Dimetrodon*, or any of its less well-known associates. *Dimetrodon* is an excellent morphological forerunner in many respects, but it is too highly specialized, especially in the vertebral spines, to be close to the actual ancestry. The same applies to *Sphenacodon* of the New Mexico assemblage.

Earlier (Olson 1962) I suggested that it might be necessary to seek the ancestry of the therapsids among the Lower Permian haptodontines. At the time these were known only from Europe. This interpretation was based primarily upon the basically primitive nature of this group, which is an assemblage of unspecialized sphenacodontids, grouped for convenience by Romer & Price (1940). Sigogneau & Chudinov (1972) show this group as basal to various primitive therapsid lines, with Old World therapsid evolution being the source of the later therapsid stocks.

Increasing evidence of close association of the Old World and New World Permian, both on physical and biological grounds, brings into serious question the idea of an exclusively Old World origin of therapsids. Likewise, similar chronofaunal structures in different regions suggest the possibility that similar evolution may have produced therapsid lines in more than one area and from

more than one haptodontine-sphenacodontine line. Lewis & Vaughn (1965) describing a haptodontine, *Culleria*, from south-western Colorado, noted its significance in this respect. Also haptodontines are now being identified in the rocks of the Upper Pennsylvanian of North America.

Evolution leading to therapsids presumably passed through the haptodontine to the sphenacodontine level and thence to the therapsid level. *Dimetrodon* and *Sphenacodon*, as well as other less well-known sphenacodontines, are examples of the intermediate level, but are somewhat specialized offshoots. The presumed sphenacodontines from which therapsids arose are not known. It appears likely that they evolved under the general conditions shown by the Caseid Chronofauna. Only where faunas have been sampled in the areas in which they lived, in the Cutler-Abo Formations and the Chickasha Formation, have representatives of a haptodontine-generalized sphenacodontine lineage been found. What we see for the most part are offshoots living under different conditions to which they are specifically adapted, the adaptations being the specializations that exclude them from therapsid ancestry.

The limitations of sampling, both faunal and geographic, are severe. Within these it is reasonable to suppose that the Caseid Chronofauna, and probably others like it, represent a somewhat upland complex in which haptodontines evolved into sphenacodontines and thence to primitive therapsids. The gorgonopsid line represented by *Watongia* is the result of this process. No remains of one of the principal groups of carnivores, the haptodontine-sphenacodontine lineage, have been found in the 'erratic' remnants of the Caseid Chronofauna. This term 'erratic' is used to refer to occurrences of remains of genera and species that are foreign to the normal assemblages of animals and not associated with normal constituents of the *in situ* chronofauna. That these carnivores were a part of the chronofauna in spite of their absence in the erratics is reasonable under the concept that, within the complex, herbivores outnumbered the predators many times over. Where the chronofauna is well known, representatives of the lineage have been found. Still, of course, existence of such a line between the Wolfcampian and the Guadalupian is conjectural.

Beyond the fairly large assemblage from northern New Mexico and south-western Colorado, in the Cutler and Abo Formations, and the Chickasha Formation of Oklahoma, the evidence of the Caseid Chronofauna comes entirely from erratics. In the present instance such genera and species occur within the geographic range and sediments of the Permo-Carboniferous Chronofauna, but are not a part of it. Such interpretations, of course, require extensive information about the primary faunas and are reliable only after thorough and repeated samplings have been made.

The principal evidence for the Caseid Chronofauna may be summarized as follows:

1. Cutler-Abo Formations (Wolfcampian)
 - a. Northern New Mexico. Large faunal assemblage, including *Aerosaurus* (varanopsid), *Sphenacodon*, *Oedaleops* (possible caseid relative), various aquatic, semi-aquatic and terrestrial amphibians and reptiles.

- b. South-western Colorado. Somewhat similar, less extensive assemblage with a more 'upland' fauna. *Cutleria* present, varanopsids not reported.
2. Lower part of Vale Formation (Clear Fork, Leonardian, Texas)
Small pocket, about 1,52 by 3,04 and 0,91 metres thick. With *Varanops*, *Casea*, and *Cacops* (unique dissorophid). Association with other types of vertebrates reported, intimacy uncertain. Some Permo-Carboniferous Chronofaunal elements present. None of 3 genera listed above occurs in 'normal' assemblages of the Arroyo or Vale Formations of Texas or Oklahoma.
3. Upper part of Vale Formation (Clear Fork, Leonardian, Texas)
 - a. Two specimens of *Casea* in single nodule, no other genera closely associated (Olson 1954, 1958).
 - b. Palate of large captorhinomorph with 8 rows of teeth (Olson 1956).
4. Middle part of Choza Formation (Clear Fork, Leonardian, Texas)
Partial skeleton of *Casea*, probably complete at deposition (Olson 1954). Not associated with other vertebrates. Not in usual Choza assemblage.
5. Hennessey Formation (Clear Fork, Leonardian, Oklahoma)
Many skeletons of *Cotylorhynchus* (caseid). Apparently floated in (Stovall, Price & Romer 1966; Olson 1968). One tooth of varanopsid character, associated with washed-in scrap of *Captorhinikos* (Olson 1970).
6. San Angelo Formation (Guadalupean, North Central Texas)
A mixed assemblage with elements from Caseid Chronofauna, and also Permo-Carboniferous Chronofauna (association uncertain). In addition, 'advanced elements' of unknown origin.
7. Chickasha Formation (Guadalupean, North Central Oklahoma)
An assemblage with *Varanodon* (varanopsid), *Watongia*, *Rothianiscus* and caseids, *Cotylorhynchus* and *Angelosaurus*. Some 'erratic' elements, as *Diplocaulus*, a member of the Permo-Carboniferous Chronofauna.

SIGNIFICANCE OF THE NORTH AMERICAN THERAPSID

I. THE CHICKASHA GORGONOPSID

The new genus, *Watongia*, sheds some light upon the problem of therapsid origins, but it also adds confusion to an already complex situation. It goes without saying, of course, that the data are insufficient for firm conclusions and that new information, which comes bit by bit, can merely point towards a better understanding. Currently new discoveries continue to suggest a complex rather than simple transition from pelycosaur to therapsid.

It is assumed in the following discussion that *Watongia* arose from a hapto-dontine-sphenacodontine lineage in the context of the Caseid Chronofauna. Temporally it is slightly younger than the San Angelo therapsids (Olson 1962) and probably slightly older than the Ocher (Yezhova) therapsids from the early Kazanian of the U.S.S.R., Figure 5 (see Chudinov 1960, 1965; Efremov 1956; Olson 1962).

Watongia is such an excellent intermediate between the sphenacodontines and gorgonopsids that it could in fact represent the actual transitional stage. In this role it represents the only known instance of such an intermediate. The suggestion of Kemp (1969, 1972) that the gorgonopsians represent a distinct line, separate from therapsids, is supported, at least as far as the Gorgonopsidae are concerned. Parallelism, of course, cannot be ruled out, but with current evidence it seems an unnecessary complication.

Watongia may be more or less at the developmental level of *Phthinosuchus* and *Eotitanosuchus* of the Russian early Kazanian. Because of the absence of comparable parts, except as the fragments of the skull of *Watongia* can be matched with the skulls of the other two, little direct comparison can be made.

The relationships of the Russian genera to each other and to *Biarmosuchus* have been the subject of much speculation and are not yet resolved. Most recently Sigogneau & Chudinov (1972) have related eotitanosuchids to gorgonopsids and biarmosuchids to ictidorhinids. So interpreted, these two families of the Gorgonopsia (following Sigogneau 1970) diverged very early, probably at what can be considered a sphenacodontine level. Boonstra (1963) considered *Eotitanosuchus* and *Phthinosuchus* as relict representatives of an earlier stock, but not themselves on the line to other therapsids. Kemp (1969) showed the phthinosuchids as a side branch of the gorgonopsian line.

Biarmosuchids show many structural resemblances to ictidorhinids and the association seems reasonable. If *Watongia* is, as argued in this paper, a very primitive gorgonopsid, then it follows that *Phthinosuchus* and *Eotitanosuchus* grouped here as Phthinosuchidae, cannot be on the line to this family. Rather, the family originated directly from a sphenacodontine ancestry, without such intermediates.

Watongia most closely resembles the less specialized members of the subfamily Gorgonopsinae, forms such as *Galesuchus* from the *Tapinocephalus* Zone and *Aelurognathus* from the *Endothiodon* and *Cistecephalus* Zones. It is, however, decidedly more primitive than any of these. It differs in many ways from members of the subfamily Rubidgeinae (Sigogneau 1970). The rubidgeines are characterized by the absence or near absence of the preparietal bone and by the exclusion or near exclusion of the frontal from the orbital margin. Although many of their features are gorgonopsian, their relationship to the gorgonopsines is not clear. *Watongia* has little direct bearing upon this problem, other than that it is a very primitive gorgonopsine, the subfamily within which the origin of the rubidgeines may lie, and that it has a preparietal and a frontal which makes broad contact with the orbit.

2. THE SAN ANGELO THERAPSID

In 1953 (Olson & Beerbower) and in 1962 (Olson) several therapsid-like reptiles were described from the San Angelo Formation of Texas. Intermittent searches in these beds, both in old sites and in new areas, have not added materially to what was known by 1962. The remains which have been recovered are tantalizing but in many ways unsatisfactory because of their incompleteness. It is, however, possible to say with confidence that in North America at the time of deposition of the San Angelo Formation there existed a wide array of non-pelycosaurian synapsids which show affinities to members of several groups of therapsid reptiles from the Ocher region and Copper Sandstones of the U.S.S.R. In 1962 these were associated as follows:

Phthinosuchids: *Gorgodon*, *Knoxosaurus*, *Steppesaurus*
Deinocephalians (Eodinocephalians): *Driveria*, *Mastersonia*, *Tappenosaurus*
Brithopodidae: *Eosyodon*
Venjukovoidea: *Dimacrodon*

These assignments still appear to be the most reasonable possible for these genera. Both the San Angelo and the Ocher assemblages indicate that extensive radiations had taken place by very early Guadalupian-Kazanian times. Neither in Europe nor in North America is there a trace of the direct source of these forms, except the probable ultimate pelycosaurian origin from very early Permian haptodontines. The only possibility, now that the association of *Watongia* and caseids is known, is that some of the genera assigned to the phthinosuchids are actually gorgonopsids, close to *Watongia* and with a source in the Caseid Chronofauna. The most likely candidate is *Knoxosaurus*, Figure 3H, which has two large canine teeth and small postcanines, somewhat a gorgonopsian pattern but one also not greatly different from that of phthinosuchids.

Except for this rather remote and indeterminable possibility, the San Angelo and Ocher forms have no known sources. We may speculate that there existed one or more unknown chronofaunal types from which they arose and that these existed outside of areas where deposition and preservation are currently known. The San Angelo complex appears to include a variety of ecological types and probably a considerable mixing of animals from different adaptive zones. Elements of the Caseid Chronofauna are present. The only sphenacodont is *Dimetrodon*, from the Permo-Carboniferous Chronofauna. It is known from specimens from two widely separated sites.

Close resemblances between some of the San Angelo genera and those from the upper Permian of the Soviet Union indicate similar sources. The postcrania of *Driveria* and *Mastersonia* are of the same general type found in *Estemnosuchus* from Ocher. They seem somewhat more primitive. The various parts of the skull, jaw and postcranium of *Eosyodon* show close resemblances to these elements in *Syodon*, from Ishevo, but are clearly more primitive. The supposed phthinosuchids seem to be at about the level of the Ocher *Eotitanosuchus*, but resemblances are at best vague. *Dimacrodon* is clearly trending in the general direction of venjukovoids, but the differences are marked. In addition to the therapsids, *Kahneria* of the San Angelo is very similar to *Hecatagomphius* of the U.S.S.R. as far as the lower jaw and dentition are concerned. Likewise, *Cotylorhynchus* and *Ennatosaurus*, caseids, have many features in common, although there are differences in cheek teeth and in skeletal proportions.

INTERPRETATION AND SUMMARY

Therapsids from the San Angelo Formation of Texas and now from the Chickasha Formation of Oklahoma have added a new geographic dimension to the analysis of the very early, primitive therapsids. The strong resemblances between some of the North American and Russian genera, therapsids, caseids

and captorhinids, indicate the existence of close geographic ties between the areas. The general circumstances may be interpreted somewhat as follows. We may suppose that the areas that have yielded fossil remains of terrestrial vertebrates lay in a continuous continental belt. This area as a whole probably was tropical to subtropical, lying more or less along the equator (see Olson & Vaughn 1970). Over the area existed a series of different adaptive zones, or habitat types. These differed from each other in general faunal and environmental characteristics. Similarities of environments within each of the several zones, as well as the differences between the zones, depended primarily upon topographic elevation and the amount and distribution of rainfall. Each of the adaptive zones was occupied by faunas which were fairly similar throughout but which had distinct local differences. In general, it appears, the topographically lowest adaptive zone lay near the seas or large bodies of water in evaporite basins and deposition was very broadly deltaic in nature.

It is probable that there were intermittent interconnections between the various local faunal units of each adaptive zone and, on occasion, between local units in different adaptive zones. This probably was accomplished primarily by particular species that developed capabilities of extending beyond the ecological system in which they originated. Patterns of crossing between systems probably were complex and it is likely that interchanges were accompanied by speciation as migrants adapted to the new circumstances which they encountered. The integrity of the local faunal units through time, as far as their basic ecological structure is concerned, appears to have been strong. Marked changes in an area were the result of replacement, not of local faunal evolution.

The vertebrates of the local ecological units form the chronofaunas. We may envisage many of these existing over the broad continental area, with suites of chronofaunas with similar characteristics occupying similar environments in different places. The ecological structure, although much the same within a single adaptive zone, appear to have been different in the several adaptive zones. In addition, the evolutionary levels were different between at least some of the zones.

This interpretation produces a model within which it is possible to view therapsid origins in ways which seem to give excellent fit to the rather meagre data now available.

From this model it follows that the development of haptodontine-sphenacodontine lines toward the therapsid level may have taken place in many areas. Relatively few of the evolving phyla would have passed the therapsid threshold and most of those that did probably would have been only temporarily successful. From the successful few came the major groups of therapsids for which we have an excellent fossil record.

Each of these major groups, to the extent that it is monophyletic, may be supposed to have originated in some local area—that is, within a particular chronofauna. Origins of the different groups probably took place at various places over the continental area and these may have been more extensive

than present records show. Species transfer between chronofaunas both within and between adaptive zones, and replacements of one type of chronofauna by another, from a different adaptive zone, undoubtedly had a part in producing the complex situations which we find in the record. Taphonomic mixing certainly tends to make more obscure an otherwise complicated record.

From the information available it seems safe to say that no therapsids arose in the Permo-Carboniferous Chronofauna and probably not in any chronofauna similar to it. We appear to have one instance in which a therapsid arose in the Caseid Chronofauna, this, of course, involving *Watongia*. During the times that these two chronofaunas existed there were others, those in which the types of therapsids recorded in the San Angelo Formation and the Ocher site originated. We have no first-hand knowledge of where or under what circumstances these origins were taking place. What indirect evidence there is, from the San Angelo and from at least some of the Russian sites, shows that materials were transported into lowland depositional sites. Presumably the chronofaunas tapped by these samplings were more upland than any for which we have first-hand knowledge of areas of habitation. Whether such areas will be found preserved, of course, is an open question; but on the basis of present information, the prognosis is negative.

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